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Dark diversity in the dark: a new approach to subterranean conservation

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Abstract

When trying to predict biodiversity patterns, species absences in a community can be as informative as species presences. The concept of dark diversity considers geographical and ecological filters to set an expected species pool and to compare it with the observed species pool, through an index known as community completeness. Completeness shows no relationship with latitude, allowing the comparison of different communities and regions concerning community saturation. Here we propose the use of these methods to a better understanding of subterranean biodiversity patterns. We applied patterns of co-occurrence among phylogenetically related species to set the theoretical species pool and then compared it with the observed richness, using isopods as model taxon. Except for one cave, dark diversity was equal or higher than observed richness. Even though completeness was low in most cases, those caves with higher completeness represent a valuable sample of regional subterranean species pool and may act as a repository of diversity. Our study showed that the dark diversity approach is adaptable to studies of subterranean communities and may be coupled with other conservation tools towards more effective management decisions.

Keywords

cave, completeness, isopods, species pool

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Introduction

Subterranean biodiversity patterns are marked by taxonomic and functional disharmony (*sensu* Cardoso 2012) and by high species turnover (Gibert and Deharveng 2002) when compared to the surface fauna in the same region. On the one side, taxonomic and functional disharmony occurs when species or functional groups are missing from the subterranean environment, because some taxa may be favoured to the detriment of other taxa during the occupation of caves (Cardoso 2012). On the other side, high species turnover reflects the smaller ranges of obligate cave fauna (Barr and Holsinger 1985; Gibert and Deharveng 2002). The processes underlying these patterns are generally attributed to regional factors, such as high habitat fragmentation and long term stability (Gibert and Deharveng 2002), and to local influences, such as resource and habitat availability, competition, and predation (Culver 1981; Christman and Culver 2001; Culver 2012; Resende and Bichuette 2016). Biodiversity, thus, bears an imprint of both influences (He et al. 2005) in such a way that species do not occur in all caves or habitat patches where their occurrences are expected (Culver and Pipan 2009; Culver 2012; Resende and Bichuette 2016). One way to understand the impact of these patterns on subterranean communities is by looking for those species whose presence was expected but are absent instead.

Observable patterns cannot always be completely explained by ecological mechanisms, because they reflect only part of the bigger picture (Lewis et al. 2017). Some species occur in the region, tolerate the conditions of the environment, but are not present in the focal area. The knowledge of this kind of absences can complement the understanding of ecological processes and increase the effectiveness of conservation strategies (Lewis et al. 2017). This concept is known as dark diversity (Pärtel et al. 2011). Understanding which species are in the dark diversity, why they are absent, and the consequences to community processes sheds light on several ecological processes still not completely understood or predicted by observed patterns of species distribution. Using dark diversity, one may better understand species distributions (Riibak et al. 2015), predict the restoration potential of degraded habitats, the likelihood of successful species invasions (Lewis et al 2017) or even future distributions of threatened species under a climate change scenario (Tang et al. 2019). Possibilities are innumerable. For example, in subterranean communities we may question the implications of dark diversity in terms of community saturation and how this information can be applied to cave conservation.

Underlying the concept of dark diversity is the idea of how much of the species pool is realised within a community (Pärtel et al. 2013). With such information complementing other methods, ecologists may adapt informed and effective strategies for conservation and restoration (Lewis et al. 2017). Calculating the proportion of species absences (dark diversity) in relation to presences (observed richness) enables one to understand which part of the observed richness is natural variation in the regional pool size and which part is dark diversity (Pärtel et al. 2013; Pärtel 2014). An index known as community completeness (Pärtel et al. 2013) allows us to estimate this proportion

and it is calculated as the logistic expression between observed richness and dark diversity ($\log_e$(*observed richness / dark diversity*)). Since species richness and dark diversity covary, community completeness shows no relationship with latitude, allowing the comparison of different communities and regions (Ronk et al. 2015).

Even though this concept of biodiversity has been encouraged and discussed since its definition by Pärtel et al. (2011), only a few studies effectively applied dark diversity to enhance the prediction power of ecological processes (e.g. Pärtel 2014; Riibak et al. 2015; Ronk et al. 2015; Tang et al. 2019) and to encourage its importance in supporting well informed management decisions (Lewis et al. 2017). Some controversy about the determination of species pool also has been raised (Mokany and Paini 2011), but methods already applied to the determination of suitable habitats, using Beals probability index based on co-occurrences (Beals 1984; Münzbergová and Herben 2004) or in Ellenberg indicator values proved applicable to dark diversity as well (Lewis et al. 2016). Despite this central role in understanding biodiversity and its importance in conservation and management, the concept of dark diversity has been applied only to plant communities, probably because of the availability of plant databases at several spatial scales. No study has applied dark diversity to subterranean communities to date. In the midst of this debate, we propose that the application of dark diversity to subterranean communities is feasible and interesting for conservation purposes.

We used an assemblage of terrestrial isopods (Oniscidea) as a model taxon for evaluating the dark diversity of caves. Isopods are a very diversified and widespread group not only in superficial but also in subterranean environments, particularly in caves, where they benefit from the milder conditions, high humidity, and the great variety of favourable substrates (Taiti 2003; Campos-Filho et al. 2014). Phylogenetically related taxa were used to set the species pool and to appropriately assess dark diversity, because only a few species of isopods co-occur inside caves (Fernandes et al. 2016). We expected subterranean communities to have high dark diversity and low completeness, because of their typically high beta diversity (Gibert and Deharveng 2000). Therefore, we aimed to compare how much of the habitat-specific regional isopod species pool was found within each local cave community. In addition, we advocate for the application of the dark diversity concept in ecological studies and monitoring of subterranean ecosystems to help guide conservation policies.

Methods

Study area

We collected terrestrial isopods from caves in the São Domingos karst area located in the state of Goiás, central Brazil (Figs 1, 2). The region is within the Morphoclimatic Domain of Cerrado (Ab'Saber 1977), predominantly with cerrado, and under tropical seasonal climate, with wet summers and dry winters (Köppen's "AW") (Alvares et al. 2014). A solid body of knowledge has been built about subterranean fauna from São

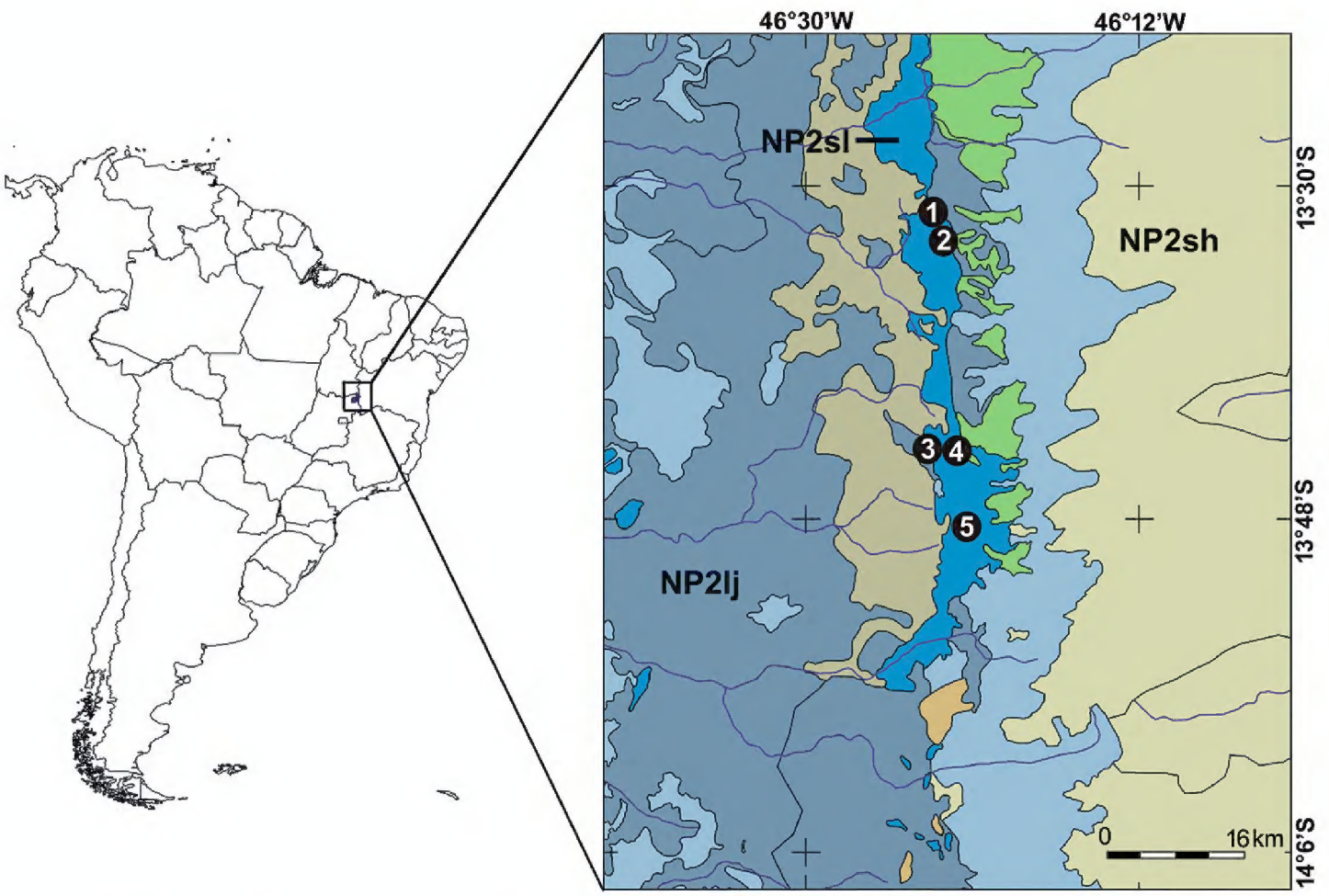

Figure 1. Caves studied in São Domingos karst area, state of Goiás, Brazil. **1.** Lapa do Angélica; **2.** Lapa do Bezerra; **3.** Lapa da Terra Ronca II; **4.** Lapa da Terra Ronca I (Terra Ronca System); **5.** Lapa São Bernardo. NP2lj = sequences of sedimentary rocks with low metamorphism; NP2sl = metalimestones intercalated with silty clay to sandy sediments; NP2sh = predominantly silty-clay sediments.

Domingos, because the region is explored since the onset of biospeleology in Brazil, in the early eighties (Dessen et al. 1980; Trajano and Gnaspini-Netto 1991, Pinto-da-Rocha 1995, Simões et al. 2013; Bichuette et al. 2019). Most published faunistic lists of subterranean fauna suffer from difficulties related to taxonomic identification and description of species (Trajano and Bichuette 2010), which prevented us from calibrating the species pool using previously published faunal lists.

Caves in São Domingos developed through dissolution of carbonate rocks by percolation of slightly acidic water. They were formed in Neoproterozoic metalimestones characteristic of the Bambuí Geomorphologic Unit, the largest set of rocks favourable to the formation of caves in Brazil (Karmann and Sánchez 1979). All caves are developed in a continuous outcrop of these metalimestones interspersed with dolomitic limestone and silty clay to sandy metasediments (Souza et al. 2004). Though subterranean connections among cave systems have not been determined as of yet, they are plausible considering the several interconnected spaces that are typically associated with this form of speleogenesis (Juberthie 2000) (Fig. 1). We elaborated the map of São Domingos using QGIS free software and shape files from Brazilian Geological Survey (CPRM 2015).

Even though São Domingos is protected by the boundaries of a State Conservation Unit (Terra Ronca State Park – PETER), the integrity of subterranean environments

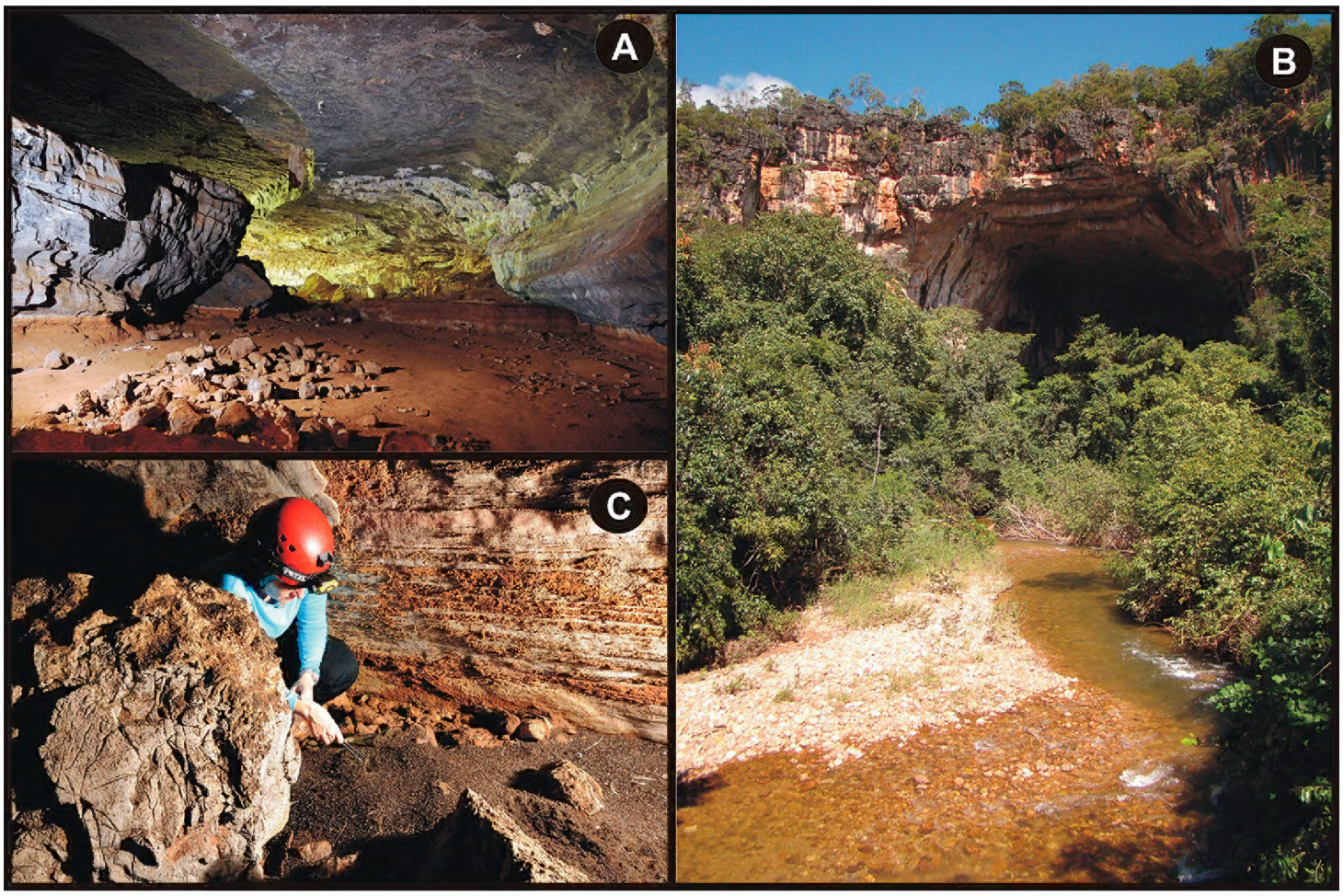

Figure 2. Representative photographs of sampled caves. **A** Lapa do Angélica (photo: A. Gambarini) **B** entrance of Lapa da Terra Ronca I (photo: ME Bichuette) **C** Guano pile inside Lapa do São Bernardo (photo: A. Gambarini).

is still at risk because portions of the headwaters of all subterranean rivers are unprotected or in close proximity to anthropogenic threats, such as soybean plantations and pastures. Therefore, the area is still affected by land ownership problems and by anthropic activities outside the park resulting in sedimentation and groundwater pollution (Simões et al. 2013).

Field sampling

We collected terrestrial isopods from early 2011 to late 2012 every three months in five caves and their surface vicinities distributed throughout São Domingos. All cave systems we visited were near each other, with the same level of environmental integrity at its environs and the same phytophysiognomy (Cerrado). They are extensive caves, with large entrances and kilometers of extension. Resources are abundant, brought by floods and bats, and so is the availability of microhabitats. We searched for isopods in several types of microhabitats. Sampling effort was ca. 4 person-hours at each site, equally distributed inside (subterranean environment) and outside (surface environment) the caves. Because of the extension of the caves, we did not collect their full length, but searching was distributed equally at each zone (entrance, twilight, transition and aphotic). Inside the caves, the search consisted of turning over rocks, logs, and debris while

inspecting every organic substrate prone to harbour invertebrates. In addition to active visual encounter surveys, we removed soil at several locations outside of each cave but within 100 m of the cave entrance and sampled leaf litter, using Winkler extractors and Berlese funnels (Palacios-Vargas et al. 2013). We took approximately ten soil samples and collected leaf litter using a shovel or hands, near the locations of soil samples. We sampled around three bags with 20,000 cm^3 of leaf litter each per cave and then, processed it in the traps while still in the field base. We deposited all isopods at the Federal University of São Carlos and sent some specimens of some taxa to taxonomists for species identification.

Estimating dark diversity and community completeness

To estimate the dark diversity (Pärtel et al. 2011) of the isopods, we defined the species pool as the set of species occurring in the study area that were potential colonisers of caves. Patterns of co-occurrence among phylogenetically related taxa were chosen to define the species pool. Accordingly, an absent species is part of the species pool if it typically co-occurs with observed species present in the community (Lewis et al. 2016). We considered the clade Mandibulata as monophyletic (Myriapoda, Crustacea, and Hexapoda), following the most recent advances in Arthropoda phylogenetic hypotheses (Giribet and Edgecombe 2012) and assumed these groups to have similar ecological requirements based on their shared evolutionary history (Webb 2000).

We applied the Beals Index of Sociological Favourability (Beals 1984), as modified by Münzbergová and Herben (2004) to exclude target species. This index estimates the probability of finding a species at a site regardless of whether the species actually occurs there. We organised the data in a composition matrix, with sites in columns, species in rows, and presences or absences in cells. Since no appropriate external database was available, we calculated Beals Index using only the data we sampled, with a total of 231 species and 1,083 individuals of Mandibulata. We used the function "beals" (De Cáceres and Legendre 2008), part of the R package Vegan (R Development Core Team 2013) to calculate the Beals Index.

To consider whether an unoccupied cave was habitable by a given species, we defined a threshold value for its suitability using the probability distribution of Beals values. To do so, we compared where in the cumulative frequency distribution of Beals values the unoccupied habitats ranked compared to occupied habitats. An unoccupied habitat with a Beals Index value below any occupied habitat would have 0% probability of being occupied, and so on. These percentiles of Beals Index can be directly interpreted as habitat suitability (Münzbergová and Herben 2004). The dark diversity corresponded to absent species of isopods with more than 50% of probability of occurring in the focal cave. Finally, we estimated the Community Completeness as the natural logarithm of observed richness divided by dark diversity ($\log_e$(*observed richness / dark diversity*)), following the logistic expression of Pärtel et al. (2013).

Table 1. Estimates of dark diversity and community completeness of isopods inside caves from São Domingos. **OR** = observed richness; **DD**= dark diversity; **CC**= community completeness.

Cave	OR	DD	CC
Lapa do São Bernardo	1	4	-1386
Lapa do Angélica	4	2	0.693
Lapa do Bezerra	1	5	-1609
Lapa da Terra Ronca I	2	2	0
Lapa da Terra Ronca II	3	3	0

Results

By comparing the Beals Index distribution at both occupied and unoccupied habitats, we set the threshold value at 0.559, which was the median of the occupied habitats. Above this Beals Index value, an unoccupied habitat had 50% of probability of being occupied, representing suitable habitats for the presence of isopods already present in the species pool.

In the five caves we sampled, we found six species of isopods. On average, only two species inhabited each cave (mean $\pm$ s.d. = 2.2 $\pm$ 1.30), with the richest cave, Lapa do Angélica, having four species. Most species were in the dark diversity (3.2 $\pm$ 1.3), even when a given species was distributed in other nearby caves. Only Lapa do Angélica had positive value of completeness, with more species present than absent; the others had negative values, with more species in the dark diversity (Table 1).

Discussion

Cerrado is well preserved and is continually present outside all caves of São Domingos, allowing dispersal of the fauna via surface environments. Subterranean dispersal may also occur via the innumerable interconnected cracks and crevices typical of the karst, because the limestone outcrops in São Domingos are continuous (Bichuette and Trajano 2003). Despite this, isopods that were widespread on surface and caves nearby did not occur in all the caves where they potentially could.

Even if each cave is unique in its shape and resource inputs, almost all caves had dark diversity equal or higher than observed richness, with low completeness. From a conservation perspective, the caves with higher completeness may be a source of migratory individuals to other areas in the vicinity, which may suffer impacts and local extinctions (Lewis et al. 2017). Therefore, Lapa do Angélica, the only cave with positive value of completeness, has the higher regional relevance, acting as a potential repository of diversity to nearby caves.

Lapa do Angélica is an extensive cave with great input of organic matter during the rainy season. In its 14 km of horizontal projection, the cave is crossed by a river with almost 7 km of subterranean routes with stretches of rapids and several rainfalls resulting

in high amount of organic matter being imported and transported from adjacent communities (Auler et al. 2001; Bichuette and Trajano 2003). These conditions provide high diversity of microhabitats and food sources for the fauna, probably enabling the coexistence of the four species of isopods found there and minimising the number of species in the dark diversity. Lapa do Bezerra, on the other hand, was the least diverse in isopods and had the lowest completeness, despite its more than 8 km of horizontal projection traversed by almost 4 km of a river with high transport capacity accumulating great amounts of organic matter inside the cave (Bichuette and Trajano 2003). Lapa do Bezerra and Lapa do Angélica are part of the same cave system (Angélica-Bezerra cave system), possibly connected to each other and both with similar altimetric gradients (around 120 meters) (Guyot et al. 1996). It is possible that their proximity influenced the expected occurrences based on shared fauna and resulted in the lowest completeness of Lapa do Bezerra, just as the isopods in the dark diversity may be part of the fauna not discovered yet (hidden diversity *sensu* Pärtel 2014). Both Lapa do Bezerra and Lapa do São Bernardo caves have river beds with narrow margins, with narrower deposits of sediments and organic matter when compared to Lapa do Angélica (Auler et al. 2001). During the rainy season, organic matter is washed away from these microhabitats and the fauna can hide in inaccessible passages of the cave. On the one hand, the community can be saturated at lower richness, because of the lower input of organic matter. On the other, some species that are present may not have been sampled yet, because of their behavior facing the conditions of the environment. Consequently, both the hidden diversity and the completeness can be influenced by the shape of the caves.

Setting conservation priorities is essential, because funding sources are finite and several societal interests are involved (Díaz et al. 2011). Coupled with already existing conservation tools, dark diversity and completeness can be a helpful tool to aid and direct conservation efforts. Through an accurate assessing of completeness, researchers and managers can evaluate and monitor restoration of degraded habitats, avoid the risk of species invasion, and direct efforts to preserve a valuable sample of regional species pool (Lewis et al. 2017). This can be especially important in areas with caves and its irreplaceable and often vulnerable specialised fauna. Understanding the local species pools and how the species are distributed in caves within a region can help to adapt conservation efforts to preserve a representative sample of the subterranean fauna, from which at least part of lost species can be recouped. Our study showed that the dark diversity approach using patterns of co-occurrence among phylogenetically related taxa is adaptable to subterranean communities and may be the kickoff for both applied and theoretical studies aiming the better comprehension of ecological processes underlying patterns of subterranean biodiversity.

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Supplementary material 1

Supplementary file

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Data type: script

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